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THE MORPHOLOGICAL ASPECT OF RESISTANCE TO BROWN ROT IN STONE FRUIT.

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The Morphological Aspect of Resistance to Brown Rot in Stone Fruit.[1]

BY

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With sixty-four Figures in the Text.

OF the many papers dealing with resistance to disease in plants that have been published in recent years, not a few have dealt with the question from the standpoint of Brown Rot of stone fruit caused by *Sclerotinia cinerea*, Schweter. Most of the work on this disease has been of a chemical or biochemical nature; some has dealt with the physical and physiological sides of the question, but few papers—only one of note—have been concerned with the morphology of the host.

The earlier papers on the chemistry of the subject were written by Cook and Taubenhaus (1), Cooley (2), and Valleau (6), while all the more recent investigations have been carried out by Willaman, either working alone or in conjunction with others (7, 8, 9, 10, 11). In nearly every case the plum was the fruit chosen for investigation. The main points which these investigations have either established or considered are: the existence of a relationship between the decrease in oxidizing enzyme content of fruits and the increase in their susceptibility to disease (1); an increase in acid content until it reached its maximum at the time of greatest susceptibility (at maturity of the fruit) (2); the possibility that in the slow development of the fungus in resistant fruits enough oxalic acid is produced by the hyphae to become toxic to them, resulting in the production of few or no spore tufts, and, secondly, that very little relationship exists between oxidase content or tannin content of fruits and resistance to the Brown Rot fungus (6); the pectin relations of the fungus (7); that the ash content, CaO, nitrogen, and ether extract are lower in resistant varieties, but not sufficiently so to constitute the limiting factors in the nutrition of the parasite, and that there is a decrease in ash, nitrogen, and calcium content as ripening proceeds (10); that the juices of resistant varieties have a higher specific gravity, a slightly higher H-ion concentration, a lower titratable acidity, and a slightly greater oxalic acid content than susceptible varieties,

[1] Investigation carried out under a research grant of the N.Z. Institute.

but that in these items the difference between resistant and non-resistant varieties are not sufficiently marked to convince one that they constitute the chemical basis of resistance, from which it was concluded that 'No hypothesis can be suggested as yet (1922) for the chemical and physiological basis of resistance in the Brown Rot of stone fruit' (9).

In most cases the papers on physical and morphological aspects of the question do not enter as fully into the subject as do the chemical papers, the earlier writers especially suggesting, rather than investigating, possible causes. Thus difference in resistance was attributed to variation in the texture of the skin (4); resistance to firmness and thickness of the skin (5); and susceptibility (in peaches) to the presence of down on the surface (5). Subsequently, when more exact examination was made, one investigator showed that 'mere thickness of skin is not the deciding factor in resistance, as the cells underlying the skin show the same relative resisting powers' (6). The crude fibre content was found by another investigation to be higher in resistant than in susceptible varieties (10), and the thickness of the skin as one of the important factors in resistance was again confirmed (9). Most recently of all, the same investigator and his colleagues have established that the higher crude fibre content of resistant varieties holds more in the ripe than in the unripe fruit; that the pentosan content shows somewhat the same relation to susceptibility as does the crude fibre, but to a less degree, and that when the two factors are added the relation to susceptibility is more marked than when either is considered alone; that although toughness of skin decreases in all varieties as ripeness proceeds, the change is more marked in susceptible varieties; that the firmness of the flesh parallels the toughness of the skin at all stages of maturity, the two factors being of conjoint importance; that when plums become ripe, and especially over-ripe, these relations tend to disappear, and at these stages practically all varieties become susceptible to Brown Rot (11).

The one important investigation on the morphology of the host is that of Valleau (6), the results of whose pioneer work still, after ten years, constitute the basis of the morphological aspect of the theory of resistance. When describing the method of entry of the fungus he states: 'It was found that the hyphae entered between the guard cells into the stomatal cavity. In those stomata lined with corky material infection of the fruit tissue does not take place immediately, as the fungus apparently has not the power to pierce directly through the corky cells. The hyphae continue to grow, filling up the stomatal cavity, and eventually exert enough pressure to split away the epidermis from the lenticel cells. It is through this opening that infection takes place into the fruit tissue. In young plums, before corky material has been formed, the germ-tubes also enter through the stomata. After entering they come in contact with normal fruit tissue, and direct infection takes place. In two of the most resistant varieties the

formation of lenticels, due to the filling of the stomatal cavity with parenchyma cells, was very common. That the complete plugging of the stomata is a factor in resistance is shown by the fact that many instances were noticed in which these stomata were completely covered by germinating spores, with no resulting infection. It did take place, however, through stomata the cavities of which were only partially filled with these cells and also through those in which only the corky tissue was present.' In his series of conclusions he says: 'Varieties show great differences in resistance to infection, owing to the production of parenchymatous plugs which fill the stomatal cavity and to lenticels made up of layers of corky cells through which the hyphae are unable to penetrate. Corky cells lining the stomatal cavity merely delay infection.' In addition to any difficulties in entry such as have already been enumerated, varieties show variation in resistance to rot after the hyphae have gained entrance, this later resistance being correlated with a thick skin and firmness of fruit after ripening. Moreover, Valleau states: 'No instances were found in which the germ-tubes gained entrance directly through the cuticle.'

Material and Methods used.

The varieties of fruit examined in the course of the present work comprise:

Plums: Monarch, Coe's Late Red, October Purple, Burbank, Japanese (var.), Yellow Cherry Plum, Red Cherry Plum.

Cherry: variety not determined.

Nectarines: Early Rivers, Goldmine.

Peaches: Kia Ora, Kalamazoo, Wiggins, Golden Eagle.

Apricots: Moorpark, Royal, Beauge, Hemskirk(e), Roxburgh.

These varieties were not chosen for their resistance or susceptibility, but because they are grown locally for commercial purposes. The writer desired to follow the history of invasion and infection in typical commercial fruits, and in particular to reinvestigate in varieties of plums other than those already described by Valleau, and to examine, for the first time in a wider range of stone fruit, the path by which the parasite enters the host. Other details of later stages of invasion are also touched upon here and there in the course of the work.

Most of the fruit was infected by conidia in suspension, and then fixed after intervals of 5, 10, 15, 20, 24, and 48 hours. The sections cut were not thicker than 5 μ. The double stain eventually used for all sections was gentian violet and orange G. Overstaining with either stain of the combination was found to be of assistance, for infected areas, while still minute and perhaps with no fungus visible in the section under examination, were thereby thrown into contrast with the surrounding healthy tissue and could be readily detected even under low magnification.

OBSERVATIONS.

Plums.

Monarch. This is an English (?) more or less resistant variety which has a well-developed cuticle, and epidermal cells of moderate size and regular form. The latter are often grouped in pairs which owe their origin to the division of former epidermal cells, by which means the epidermis is partly enabled to keep pace with the enlargement of the tissues below. Five to seven layers of firm-walled cells with only small intercellular spaces lie between epidermis and flesh, and with the former comprise a skin which for a resistant variety is comparatively thin. The cells of the outermost layer of hypoderm are not much larger than those of the epidermis, but in the succeeding layers the size is consistently and greatly increased. All the cells of the hypoderm, especially near stomata, where they are shallower than elsewhere, are elongated parallel to the fruit surface. When further expansion of the superficial layers of the skin than that afforded by division of the epidermal cells is required, small isolated groups of cells of the outermost row of the hypoderm increase in size, at the same time stretching the epidermal cells above them until the upper and lower surfaces of the latter touch and finally break. A new cuticle meanwhile forms over the enlarging hypoderm area and its cells henceforth serve as epidermal cells, gradually rising into the plane of the epidermis and becoming almost indistinguishable from normal epidermal cells except at the periphery of the area, where a slight depression is usually noticeable. The slight depression in the early stage over this secondary epidermis, together with its marginal rim, helps to retain conidia in position, while its thinner cuticle offers a readier way of ingress than the normal cuticle affords. From the point of view of fungal invasion, therefore, secondary epidermis is at least a temporarily weak area.

Stomata are distinctly rare. The chamber is large but relatively shallow. When the fruit is young the chamber is usually open, but in many stomata a cone of cells is developed as the fruit matures, and this eventually may also fill the cavity. As the cavity is broadly conical in shape a narrow passage is left for a short distance between the side of the cone and the epidermal cells above, and invading hyphae experience little difficulty in following the path thus left open for them.

Both stomatal infection and direct infection (i. e. straight through the uninjured cuticle) occur in this variety of plum. If conidia lie within a short distance of a stoma, stomatal infection is bound to take place. The germ-tubes, for several usually enter either simultaneously or in quick succession, grow freely into the stomatal aperture, pass down between the guard cells, and as a rule then pass out among the hypoderm cells by way of the cells abutting on the channel at the side of the cone. If the stoma is well blocked

the hyphae may be delayed before they succeed in reaching the hypoderm, but the delay is only temporary.

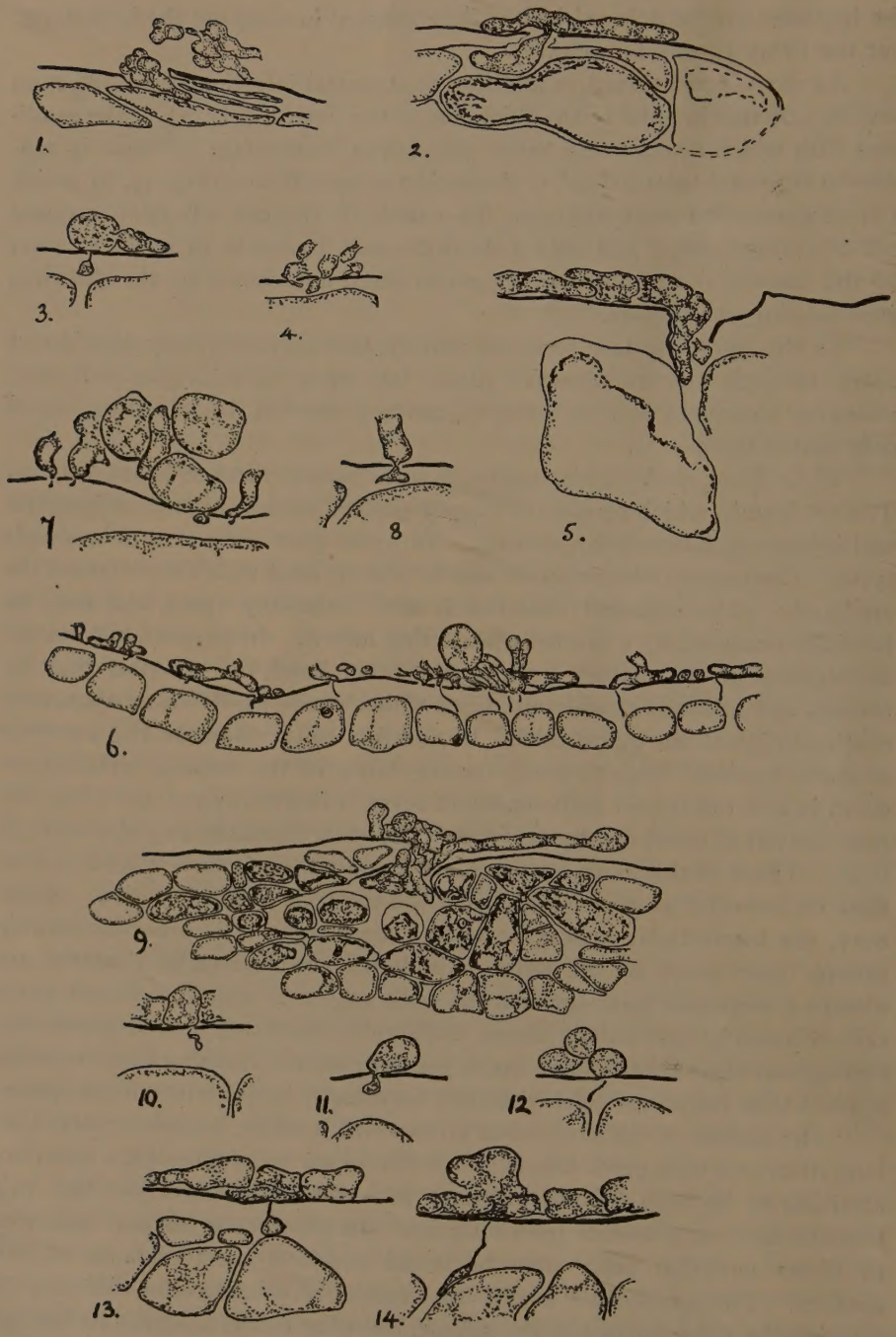
As already mentioned, in addition to stomatal infection, direct infection occurs, and this in spite of the thickness of the cuticle (Fig. 1). The readiness with which direct entry takes place, even in the face of what is considered stomatal 'attraction', is shown in the next figure (Fig. 2), in which a stout germ-tube has penetrated the cuticle of the cell adjoining a guard cell of a stoma, yet it had only a short distance to travel in order to enter by the mouth, down which other germ-tubes, not shown in the drawing, were passing at the time.

In this more or less resistant variety, therefore, not only does direct entry through the cuticle take place, but entry through the well-filled stomatal chambers is only delayed, never prevented, by the plugging of cells within them.

Coe's Late Red. This, again, is an English, semi-resistant variety. The epidermis, which consists of closely packed cells, is broken at irregular and infrequent intervals by stomata. In green fruit these are of a simple type. The guard cells are small and lie almost level with the surface of the epidermis. The stomatal chamber is also noticeably small, and may be partially occluded by a few cells projecting into it. In some of, but not all, the stomata of the mature fruit, on the other hand, the chamber may be almost, and at times completely, filled with a cone of cells whose apex may reach as high as the guard cells. In addition to the stomata the presence of small lenticels helps to break the regularity of the surface. The hypoderm is well developed and consists of seven or eight rows of cells, but the rows are not of equal resistance, for only the outer four or five consist of small cells. Those of the inner rows are large, and although their walls are firm they do not offer as great resistance as do the cells of smaller size. Moreover, the intercellular spaces between these larger cells are considerably greater than those of the outer hypoderm, and intercellular spaces are always a weakness, however firm the walls may be. For this reason small cells of more or less oblong shape, with walls which are united practically throughout their length, have much greater power of resisting the advance of hyphae than have oval cells with their necessarily larger intercellular spaces.

The surface of the fruit, when strewn with conidia, becomes covered for long distances with germ-tubes. Well-developed examples of the latter are at times to be seen in close contact with the cuticle, and yet the fruit beneath them may be free from infection. In other cases several instances of direct cuticular entry may be found within a short distance of one another. The germ-tube seems to experience considerable difficulty in piercing the outer surface of the cuticle, but once this is achieved its further growth is not obviously hampered (Fig. 5).

As is usual in surfaces that bear stomata, stomatal entry is common,



FIGS. 1–14. Plums. Figs. 1 and 2. Monarch. 1. Direct entry through cuticle of epidermal cell. × 440. 2. Direct entry through cuticle of cell supporting a guard cell of a stoma, the open stoma mouth evidently exerting no directive force even at this short distance. × 985. Figs. 3–5. Coe's Late

and in the present variety the plug of cells within the stomatal chamber offers no permanent barrier to the ingress of the germ-tube even though, as in some of the stomata examined, the cone of cells, or in the simpler type the intruding hypoderm cells, are sufficiently developed to almost close off access to the parts below the guard cells. One feature in this variety, however, in connexion with the frequence of stomatal entry, is of significance. The stomata are not evenly distributed, but are irregularly grouped. Now since the total number of stomata in the variety is small, irregularity of distribution necessarily involves the existence of relatively large areas without stomata. As has already been shown for Monarch and the present variety, and as will be shown for all the other plum varieties examined in the course of this work, stomatal invasion never fails to take place if conidia only lie close enough to the stomata, whatever the internal structure of the latter may be. That there shall be large areas without stomata is therefore a factor of primary importance in warding off invasion. The number of stomata occurring in a group is of secondary importance only, provided the total area of the group is not large. For the infection of one stoma will lead to invasion which in most varieties will involve the whole fruit in time ; the infection of two or more stomata at once only hastens decay.

A slight check is experienced by the hyphae after entry, whether they have entered directly or through the stoma, and it is exerted by the outer half of the hypoderm. Their advance in this region is at a moderate pace only. Nevertheless they are well developed, and branching occurs at sub-distant intervals. Repeated branching at close intervals is characteristic of growth within resistant tissue, and this hypoderm is therefore not to be regarded as strongly resistant.

The chief agents conferring resistance on the variety are the rarity and the grouping of the stomata, and consequently the small total number of stomatal entries, together with the possession of a semi-resistant cuticle, while a third but subsidiary means of assistance is afforded by the firmness of the hypoderm.

October Purple Plum. This again is a resistant English variety, having a small-celled epidermis and a hypoderm of eight or nine rows. The cells of the latter are also small, especially those of the outer five or six rows. Intercellular spaces in the hypoderm are never large in the outer rows, and seldom so in the inner. The cuticle, as in most English varieties of plum, is stout, and its uniformity seems not to be broken by the occurrence of new, thinner areas over secondary epidermal tissue. The practical effect on the numerical paucity of stomata is further enhanced by their irregular grouping.

Red. 3 and 4. Direct entry through cuticle, early stages, but slow progress (twenty-four hours after innoculation). × 985. 5. Direct entry, later stage, germ-tube passing down middle lamella between two epidermal cells. × 985. Figs. 6, 7, 8. Burbank. Direct entry through cuticle. Magnification × 440, × 985, × 985 respectively. Figs. 9–14. Japanese. 9. Stomatal entry. × 440. 10–14. Direct entries of same age as stomatal entry shown in Fig. 9. × 985.

The stomatal chambers are usually large, but they are completely filled with a cone of delicate-walled cells which culminates in a projection of its topmost cells into, but not beyond, the channel between the guard cells. In some stomata in the material examined meristematic divisions had begun in a few cells of the cones, but the fruit when preserved was already ripe, though firm, so lenticel formation by this means is probably not general by the time the fruit becomes even soft-ripe. The stomata are freely infected and the germ-tubes appear to have no difficulty in causing the separation and collapse of the cone cells in front of their advancing tips. Indeed it would be surprising if difficulty were experienced in separating these cells, for the upper ones at least are very delicate, although the lower cells, which in most cases are older, have rather firmer walls.

Direct infection also takes place. The resistance of the variety, as far as could be determined, seems to lie in the rarity and the grouping of the stomata, and in the resistant qualities of cuticle and hypoderm.

Burbank Plum. The most obvious characteristic of this variety is the depth of the hypoderm, which may consist of as many as twelve rows. All the cells are elongated parallel to the surface, especially those of the middle rows. As in many other varieties the cells of the two outermost rows are considerably smaller than those of the others. But the hypoderm as a whole is divided into an outer and an inner part, the former having six to eight rows of smaller, firmer-walled cells, while in the latter the cells are much larger and thinner-walled, yet are still noticeably firmer than those of the flesh below. The epidermis consists of small regular cells, all of whose walls are of about equal length.

Another characteristic of the variety concerns the distribution of the stomata. They are rare, yet so unevenly are they distributed that a false impression may be gained by examining only a few isolated samples. When the fruit is mature most stomata have their cavities plugged with thin-walled cells, and in some cases this process is so complete that one or more cells pass between the guard cells and project beyond the mouth of the stoma. When lenticels are formed, as they not infrequently are, rapid division takes place in the lower layers of cells plugging the stomatal cavity. The guard cells are eventually forced apart, but several divisions may previously occur in the epidermal cells bearing them, as if in an attempt to keep pace with the expansion below. Eventually, however, the guard cells are widely separated, and in a mature lenticel, when its surface is fully exposed to the exterior, it is not always easy to trace its stomatal origin.

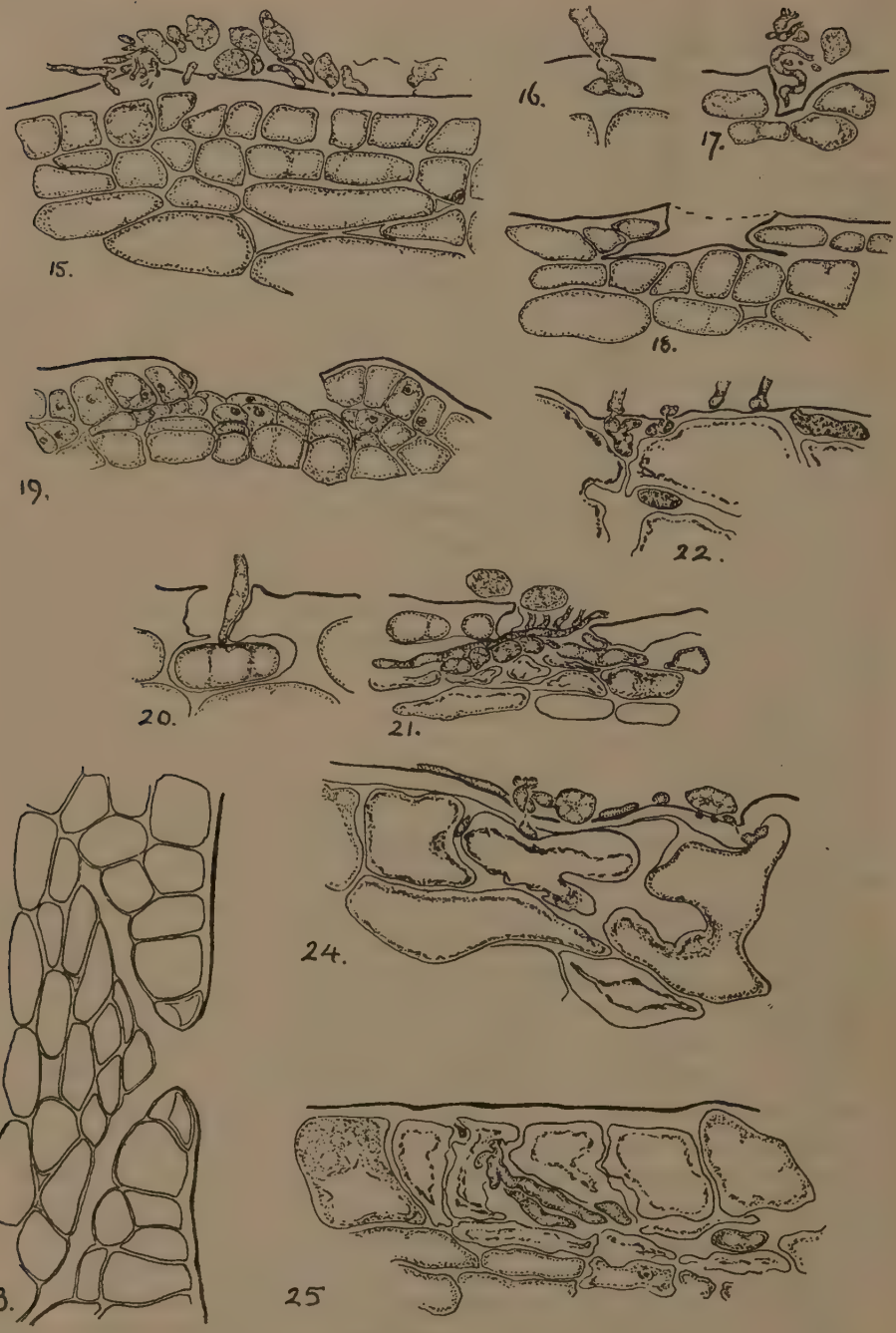
Expansion of the skin is due partly to division of the epidermal cells and partly to the rise of the hypoderm cells in small areas, taking the place of the two or three epidermal cells that previously covered them. Figs. 6–8 give an indication of how frequently and how freely direct entry may take place. The absence of long germ-tubes before entry is also note-

worthy. Yet no direct entry in a plum is as rapid as stomatal entry, and even in this variety the cuticle is resistant to a certain extent. The presence of thinner cuticle over hypoderm cells that are replacing epidermal cells also facilitates direct entry when the conidia happen to lie on such areas. Some of the infected areas in the material examined in this variety were small and some large, according to whether the infection was single or multiple. Where multiple infection through an aperture had occurred it was not always possible to tell whether the original invading hyphae had entered through a stoma or directly through the cuticle. Most stomata in the mature fruit of this Burbank variety are of the type with completely plugged apertures which Valleau believed germ-tubes were unable to enter. Those which are not completely are at least well plugged, and according to Valleau's theory of resistance there should be appreciable delay in effecting stomatal entry through them. But in the present examples of multiple entry the ingress of the hyphae is obviously vigorous. If the original entry in these cases were stomatal, then either (as is probable) a so-called resistant type of stoma has been freely entered or a semi-resistant one has; if on the other hand the original entry were cuticular, its occurrence so freely serves to confirm in striking manner what can be demonstrated in every variety of plum treated in this work, namely, that cuticular entry occurs, and in some cases is formidable. This Burbank plum therefore shows that at least one of the postulates of Valleau's theory of resistance cannot be applied generally.

Progress within the hypoderm is uneven. The hyphae even after multiple infection do not grow freely in the stout outer layers of hypoderm, and even those which strike sideways may not penetrate far. Those, however, which maintain a downward course, and so soon reach the inner layers of the hypoderm where the resistance is less, fare better and grow more freely.

Japanese Plum. In this variety the epidermis consists of small cells, while the hypoderm comprises as many as seven rows. Usually, however, there are not more than four, or possibly five, rows in which the cells are small, and the hypoderm as a whole must therefore be regarded as rather weak. Each stoma is surrounded by smaller, but elongated, unusually shallow hypoderm cells with their longer axis directed towards the stoma. In the smallness of many of its cells, therefore, the hypoderm might be regarded as resistant, but the effect is largely nullified by the fewness of the rows in which such cells occur.

Stomata occur freely in some examples and less freely in others. In the mature fruit the stomatal cavity is completely filled with a broad cone of cells which reaches the base of the guard cells but as a rule does not pass between them, although examples have been seen in which a single cell at the apex of the cone projects into the guard-cell channel. The stomata of this variety closely approach Valleau's resistant type, but the fungus has no



FIGS. 15–25. Figs. 15–18. Yellow Cherry Plum. 15. Part of a group of conidia showing direct entry; $5\frac{1}{2}$ hours after inoculation. × 440. 16. Direct entry; $5\frac{1}{2}$ hours after inoculation. × 985. 17. Conidium and germ-tubes caught in irregularity of surface, and direct entry thus facilitated.

difficulty in penetrating these undoubtedly well-plugged chambers, and it is common to find a mass of hyphae, after having passed down between the guard cells, occupying the upper part of the chamber, while the cells of the cone lie collapsed below.

When within the hypoderm growth of the hyphae is rapid and their diameter wide. As they sweep freely among the cells the latter collapse at a considerable distance, both in advance and to either side of them. From the point of view of resistance the hypoderm is therefore weak.

Direct entry is common but slow. It is sometimes delayed by growth of the germ-tube over the surface before entry is attempted, and when this is begun it is further delayed by slow progress through the cuticle. Figs. 9–14 are drawn from examples in one infection drop, so the time at which the spores, or germ-tubes, reached the surface would be approximately the same. They show how completely one stomatal infection can eclipse many direct entries, and of what significance it is to the fruit that it should not be too well equipped with stomata. The average number of stomata in the variety is about one to every four–six sections 0·5 cm. in length and 5 μ thick. Summarizing the factors for and against immunity in this variety, we have more stomata than is desirable, a moderately resistant cuticle, and a rather weak hypoderm. And the result, in spite of 'resistant' stomata, is a susceptible variety.

Yellow Cherry Plum. This variety of plum, when ripe, is notable for its extreme rarity of ordinary stomata. Rapid expansion takes place in the general cells of the flesh when the fruit is approaching maturity, and a corresponding enlargement becomes necessary in the skin. This is achieved partly by a widespread division of the epidermal cells, which are consequently usually grouped in pairs, with a thicker side-wall between any two pairs than between the two members of a single pair. Expansion on a larger scale, however, is secured by the usual method of enlargement of cells of the outer row of the hypoderm, with consequent distension of the epidermal cells above the expanding area. The hypoderm cells concerned may lie beneath ordinary epidermal cells or within the stomatal chamber. In either case the distension of the epidermal cells becomes so great that all trace of them is lost, and the evidence of the origin of the new epidermis is thus removed. The frequent occurrence of these expanding areas with their thin covering of cuticle is the chief weakness of the surface from the point of view of invasion. When the expansion is beginning, also, there is an appreciable depression where a normal epidermal cell joins the distended

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× 440. 18. Mid-stage in the rise of hypoderm tissue to form secondary epidermis. × 440. Figs. 19–21. Red Cherry Plum. 19. Guard cells being pushed apart. × 440. 20. Direct entry on to top of epidermal cell. × 985. 21. Direct entry through cuticle, multiple infection. × 440. Fig. 22. Cherry. Direct entry, vigorous growth. × 440. Figs. 23–5. Nectarine, Early Rivers. 23. Conical plug of cells in stoma. × 440. 24, 25. Two stages in direct entry. × 440.

tissue, and this in itself is a weakness. Apart from these areas, however, the cuticle is stout.

No case of normal stomatal infection was found, but great numbers of cases of direct infection, both through normal cuticle and through the thinner cuticle over areas of secondary epidermis, were seen. Doubtless in firmer, younger fruit stomatal infection takes place in the ordinary way, at that stage the stomata containing cones of tissue but not being wholly plugged.

Fig. 15, five and a half hours after applying the conidia, shows numerous cases of direct infection, and in Fig. 16, also after five and a half hours, the robustness of hyphae after entry is evident. Fig. 17 shows how useful irregularity in the surface can be in assisting infection. This is an early stage in the formation of secondary epidermis, and Fig. 18 is a later stage in the same process.

As is evident from Fig. 15, the cuticle may be attacked immediately after the germination of the hyphae, which would seem to signify that the cuticle, even when of full depth, is readily pierced. Other examples however showed greater development of germ-tubes before entry was effected.

The hypoderm in this variety is thin, being usually four, but in places five, cells deep.

Owing to the absence of normal stomata in the ripe fruit and the presence of a weak hypoderm, any resistance exhibited by the fruit is to be attributed to the cuticle. This, however, is by no means as resistant as might be desired, and the reputation for resistance enjoyed by the variety is probably due to its early maturity rather than to any inherent power of disease resistance.

Red Cherry Plum. The epidermal cells of this variety resemble those of the Yellow Cherry Plum, but stomata of the normal type are present at regular, distant intervals. The stomatal chamber is usually of moderate size, and at maturity is filled with a cone of cells which may or may not project between the guard cells. The cells of the stomatal chamber may become meristematic and give rise to a lenticel proper, or a pushing apart of the guard cells somewhat as in the Yellow Cherry Plum may take place. But traces of the guard cells and of stomatal characteristics are usually still evident even when the process is more or less complete (Fig. 19). In some cases the epidermal cells covering the stomatal chamber are also stimulated to division and a complete semicircle of meristematic tissue then results. The delicate-walled cells of this tissue are particularly subject to infection, although the corky ones are not.

Stomatal infection, as usual, takes place wherever conidia happen to lie within a short distance of the aperture, but direct entry is much commoner. Yet germ-tubes frequently travel over the surface for an appreciable distance before they succeed in piercing the cuticle. Once the breach has been made in the upper circle of the cuticle, however, the growth of the germ-

tube is vigorous even before emerging from the lower cuticular surface (Fig. 20, 9½ hrs.). And once below the epidermis it is as strong after direct as after stomatal entry, especially if other germ-tubes follow in succession through the same breach (Fig. 21, 9½ hrs.).

The hypoderm in the Red Cherry Plum is slightly deeper than in the Yellow, but even so it can hardly be said to be stout. Nevertheless it exercises a marked influence on invading hyphae, which, though of moderate diameter and seemingly thoroughly healthy, do not advance as rapidly as might be expected. Growth in fact is close, not free, and compact areas of infected tissue therefore result. The direction taken by the hyphae lies more often parallel to the surface than away from it, and therefore, for a time at least, they tend to be confined to the firmer hypoderm tissue.

Cherry.

A single susceptible variety of cherry was used for the series of infection experiments, but its name could not be determined. The epidermal cells are very large and are square to oblong in section, the longer axes being parallel to the surface. The cuticle seems no thinner than in the average variety of plum, but the hypoderm, with the exception of the two outermost layers, is scarcely distinguishable in size of cell or delicacy of wall from the cells of the general tissue below. Stomata are to be found throughout, but they are rather irregularly scattered and are not really numerous. They are of simple type. The cell supporting the guard cell is of the normal form of epidermal cell. The chamber is small, and what little space there is is further reduced by the occasional presence of a few thin-walled cells. According to the older theory for plum susceptibility, therefore, the structure of the stomata, together with their occurrence in moderate numbers, is sufficient to justify an expectation of susceptibility based on stomatal characteristics.

As a matter of fact, stomatal infection in the present material was not responsible for one-quarter—nor one-eighth—of the total number of diseased areas which occurred. Stomatal infection certainly took place whenever a germinating spore lay within easy reach of the aperture. But in this case 'within easy reach' means not farther away than the width of two epidermal cells, for beyond that distance the germ-tube finds the adjacent unbroken cuticle of greater attraction than the more distant stoma mouth. In this variety of cherry, therefore, direct entry is by far the more common of the two methods. Indeed several instances have been seen in which an uninfected stomatal area was, as it were, an island of firm tissue in the midst of diseased, collapsed cells whose infection had been due to direct invasion through the cuticle. Little or no delay occurs in piercing and penetrating the cuticle (Fig. 22), and in cases where infection was general the invasion due to stomatal infection was no more advanced than that of neighbouring

areas due to direct infection. Once below the epidermis, the fungus grows at a remarkable pace. In this material the twofold nature of susceptibility is most noticeable. To begin with, there is no difficulty in entering, so the possible first limiting factor is absent. There remains the second possible limiting factor of obstruction by hypoderm or flesh by means of the physical or chemical nature of the cells. In the present variety of cherry any such resistance of the flesh against the invader is conspicuously absent. On the contrary, the host cells collapse far in advance of the hyphae, which are thus provided with an open path and an unfailing supply of nutriment.

Nectarines.

Early Rivers. Very large, square, firm-walled cells with a thick cuticle comprise the epidermis of this variety of nectarine. The hypoderm is several rows deep, and contains cells which are smaller and have firmer walls than those of the general flesh. As a rule, stomata are moderately numerous only. They usually contain a conical plug of cells whose apex rises to the two, unexpectedly small, guard cells (Fig. 23). The size of the latter presents a contrast to that of the large epidermal cells which bear them. Although these stomata are of the plugged type, and according to the older theory should be infected only with difficulty, yet they were found to be freely infected and to offer no adequate barrier to invading hyphae.

In addition to stomatal entry, however, direct entry is even more prevalent, a ratio of twenty direct entries to one stomatal being probably quite within the average (Figs. 24, 25). Yet the epidermis seems to offer slightly more resistance to penetration than it does in Goldmine, the second variety of nectarine examined.

Progress within the flesh of the Early Rivers variety, as in most nectarines, is free and vigorous, whatever the route the germ-tubes may have followed when entering.

Goldmine. There is little difference in the anatomical structure of the skin of this variety and that of the preceding, except that the hypoderm consists of slightly smaller cells. Stomata, however, are more numerous in the present variety, and although many are of the conically plugged type, in others the growth of the cells within the cavity is carried farther, resulting in the formation of a structure more of the lenticel type. Some of the superficial cells of these structures are corky and offer considerable resistance to any invading germ-tubes. At the periphery of these areas, however, the cells are of more normal constitution, and germ-tubes have little difficulty in entering there. The irregularity of the fruit surface caused by the presence of these lenticels serves to retain the conidia in position, and to a small extent they are therefore an indirect source of weakness.

Direct entry through the cuticle, on the other hand, not only takes place, but seems to be almost as rapid as stomatal entry. Moreover, it

occurs in great numbers in all infected material (Figs. 26, 27). Nearly all direct entries result in the infection of areas quite as large as those due to stomatal infection, and growth within them is as swift and vigorous as in the latter. And as twenty to thirty direct entries of major significance take place for every stomatal one, it is the former alone which really determine for the variety the question of its susceptibility.

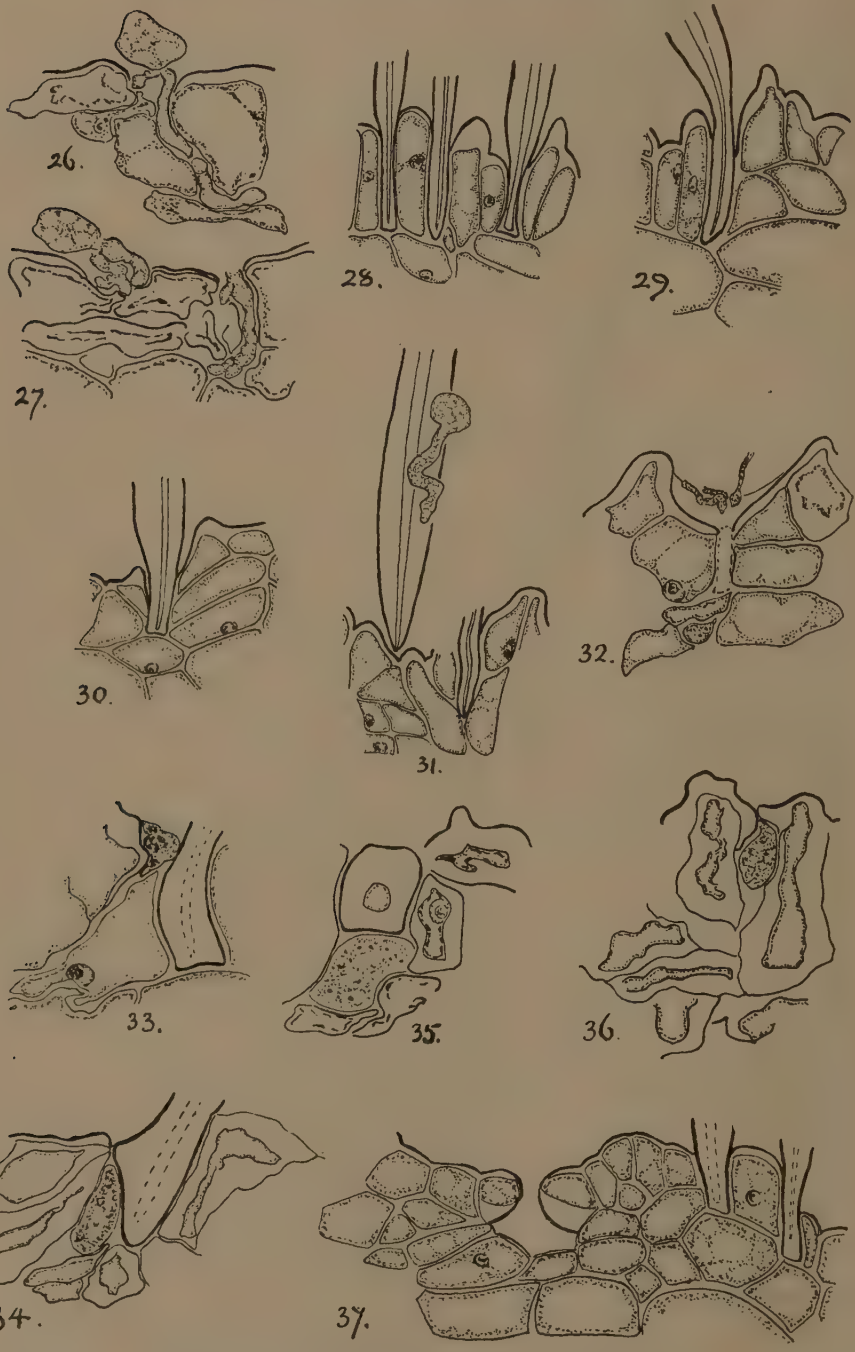
Peaches.

Kia Ora. The hypoderm of this peach is about twelve cells thick, and, except in their smaller size and greater firmness of wall at maturity, it is hardly to be distinguished in structure from the general tissue below. Most cells, both of the hypoderm and of the interior, are well rounded, but those of the two layers of hypoderm adjoining the epidermis are distinguished by being somewhat elongated.

The rarity of stomata in this peach is remarkable. The guard cells are small, triangular, and have a very thick lower wall. The chambers are of moderate size and are partially closed by irregularly arranged, delicate-walled cells of various sizes, some of which almost touch the guard cells. In spite of the presence of these cells in most stomata, there are usually air-spaces between them, so the stomatal chamber cannot be described as stuffed. Ingress and the further development of hyphae take place freely through them, and, as in the plums already described, stomatal entry takes place without fail whenever conidia lie within the requisite distance of the aperture. But there are so few stomata that infection by this means is negligible, unless a diseased fruit is in contact with a healthy one over a considerable area. In the case of fruit liable to be infected only by more or less isolated, wind-borne, or rain-splashed conidia, stomatal entry may be ignored.

The real weakness of the peach skin lies in its hairs, as most growers recognize without knowing the reason. The hair is a long narrow cylinder with an excessively thick wall and a narrow protoplasmic core extending from one end to the other. It is simply a single epidermal cell of unusual form, and is inserted at the same level as the normal epidermal cell. The part at the base, lying between the adjoining epidermal cells, is narrower than the free upper part and forms a slender stalk. Two to five epidermal cells usually lie between any two hairs, but occasionally the interval is greater, and less often it is smaller. At times also several hairs, even to half a dozen, may stand side by side without any epidermal cells between them. The insertion of two or more hairs into one socket may also be seen here and there.

When hairs stand close together, at an interval of one or two cells for instance, the intervening epidermal cells are usually tall and narrow (Fig. 28); when several cells intervene the middle ones are tall and the others shorter, the group thus forming a cushion that dips on either side



FIGS. 26–37. Figs. 26 and 27. Nectarine, Goldmine. Direct entry, growth free and vigorous. × 440. Figs. 28–36. Peach, Kia Ora. 28. Tall narrow epidermal cells between closely set hairs of epidermis. × 440. 29, 30. Hair bases inserted at side of epidermal 'cushion' several cells in

towards the hair. These cushions in part may be more than one cell deep, and the stalk of the hair then touches one to several cross-walls between the fruit surface and the base of the hair stalk (as in Figs. 29, 30). Whether one or two cells, or a cushion of cells, lie between two hairs there is always a slight depression, V-shaped in cross-section, immediately surrounding the hair at its point of insertion at the surface. It is into this depression that the tip of the germ-tube is usually directed when infection is about to take place.

The hairs, being numerous, more often than not hold the conidia a short distance above the surface, and as the air beneath the hairs is still, conditions are favourable for germination. The result is that the majority of conidia germinate while suspended above the surface, and as they are probably either resting on, or wedged between, hairs, the germ-tubes sooner or later follow the nearest line of support and travel down the hair surface.

The course of the germ-tubes is seldom straight. They may partly encircle the hair or even descend in an irregular spiral (Fig. 31). Eventually they approach the surface of the epidermis, when they either leave the supporting hair or continue for the rest of the way down it. In the former case they may grow for a short distance over the epidermis, but they soon come in contact with another hair, and finally the tip of the germ-tube bends down into the V-shaped depression surrounding the hair base (Fig. 32). After the surface is pierced at the point of insertion of the hair the subsequent direction of growth maintained by the hypha depends largely on the shape and arrangement of the epidermal cells adjoining the hair socket on the side at which the fungus enters. If there is only one epidermal cell running the full length of the hair stalk, the hypha will continue down the stalk before leaving the socket. But if the epidermal cells are part of a cushion and their basal walls are set at an angle to the socket, or meet it horizontally, the hypha may turn from the socket before reaching the base and pass down, or along, between the cells of the cushion. In Fig. 33 the hypha is turning aside at the top of the socket, which is unusual, but in Figs. 34 and 35, one of which is cut at an angle to the hair and the other transversely to it, the hypha has followed the more usual course to the bottom of the socket before turning into the general tissue.

Infection by way of a hair stalk is the common method in this variety of peach. Infection directly into the epidermis at a distance from a hair

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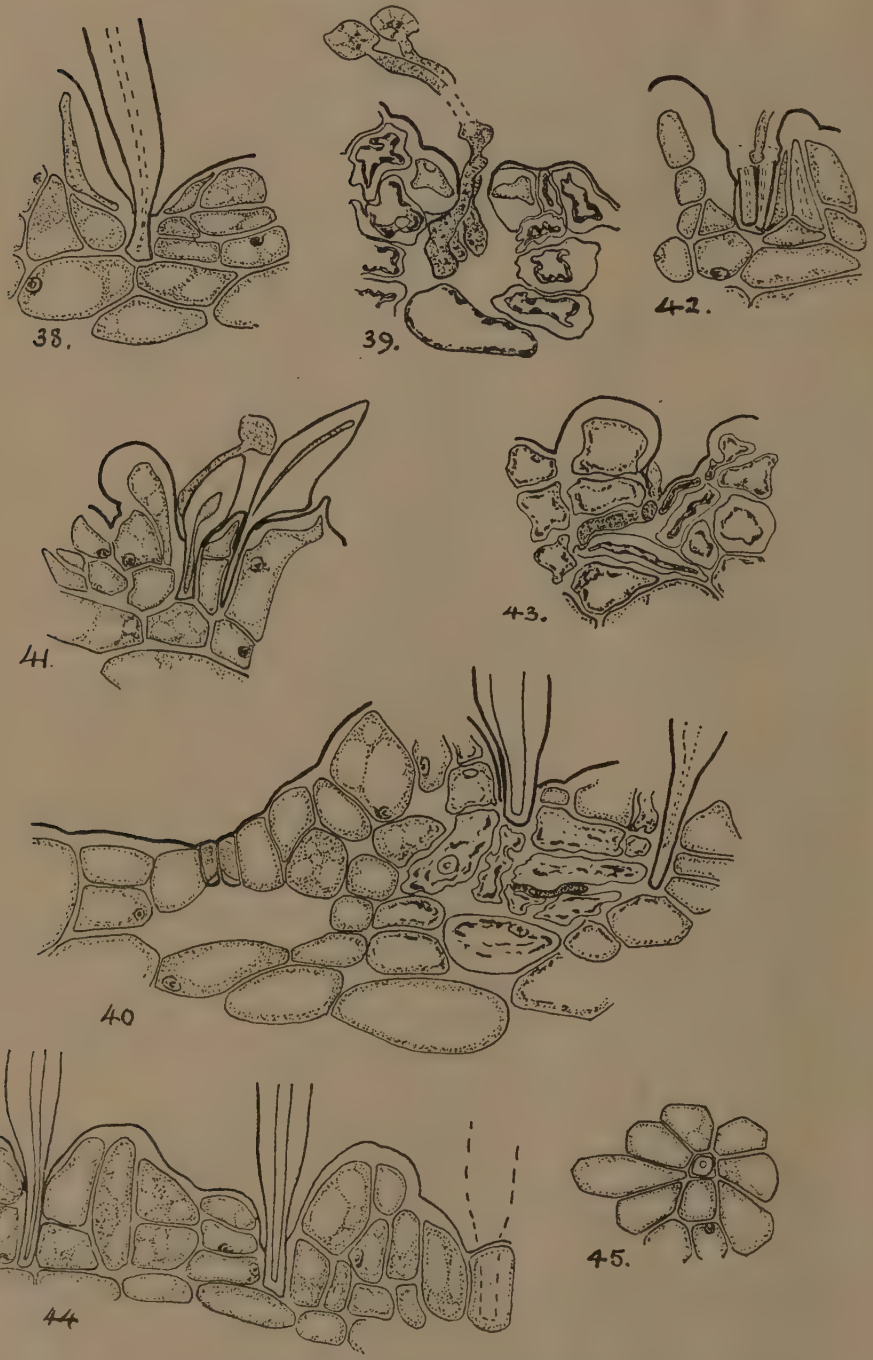
depth. × 440. 31. Germ-tube descending hair on which the conidium is resting. × 440. 32. Germ-tubes growing down the depression surrounding a hair base; hair removed, socket of stalk shown. 33. Germ-tube has entered at hair socket, but has turned aside early into the middle lamella of an adjoining epidermal cell. × 985. 34. Hypha emerging from foot of hair socket; section oblique to hair. × 985. 35. Emergence of hypha from foot of hair; latter cut transversely. × 985. 36. Hypha which has entered directly through the cuticle and not by way of a hair socket. × 985. Fig. 37. Peach, Kalamazoo. Insertion of hair base and stoma, showing relative positions. × 440.



FIGS. 38–45. Figs. 38–43. Peach, Kalamazoo. 38. Hair insertion. × 440. 39. Stomatal entry. × 440. 40. Stoma close to an infected hair base, yet itself not infected. × 440. 41, 42.

takes place occasionally, as shown in Fig. 36, but it is almost as rare as stomatal infection.

Kalamazoo. There are fewer hairs in this variety than in Kia Ora, but they are still numerous, and cases of two or more being inserted in one socket are quite common. But the spacing of the hairs is less regular, and the presence of more stomata adds to the irregularity of the surface arrangements. As in the preceding variety, the narrow, upright, elongated epidermal cell is often to be seen adjoining a hair, and cushions of cells rising above the general level of the surface are still of frequent occurrence. But in the present variety the hairs are occasionally inserted on the cushions, the depressions at the side of the latter then being usually occupied by stomata. Even the hairs inserted in the cushions, however, have at least a slight dip at their point of insertion (Figs. 37, 38).

On the whole there is a greater tendency in this variety for the cells adjoining the hair-sockets to be arranged horizontally one above the other, and it is therefore usual to find one or more cross-walls adjoining the hair stalk.

There are not usually fewer than eight hairs between any two stomata. The guard cells of the latter are rather small, and the chambers vary from almost negligible in size to large and open, often, though not always, being without occluding cells. Both in the number and form of the stomata facilities for entry and infection are offered the fungus. That infection by this route is ready is shown by the freedom of growth of the germ-tubes in Fig. 39, which is a typical example of stomatal entry for the variety. Nevertheless, stomatal entry is the exceptional rather than the common mode, that by the hair socket being the more usual in this variety as in the preceding. If any chemical attraction is offered the germ-tubes by the stoma, it cannot be felt far from the latter, for hair infection in the presence of uninfected stomata only a few cells away is by no means of rare occurrence (Fig. 40). Early, mid, and final stages of socket infection are shown in Figs. 41, 42, 43, respectively. The germ-tube follows the same course as in Kia Ora and may leave the socket at the junction of cross-walls in the adjacent epidermal cells, or, if there are no cross-walls, continue to the socket-base. It is noteworthy, not only in this variety but in most hairy stone fruit, how quickly a hair shows the presence of a fungus by collapsing at its stalk. The process of infection by way of the hair base is rapid and seems to be very little, if at all, slower than that through the stoma. Nine hours is sufficient for the conidia to germinate and infection to be established.

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43. Early, mid, and late stages in socket infection. × 440. Figs. 44 and 45. Peach, Wiggins. 44. Typical piece of epidermis showing hair insertion and arrangement of the epidermal cells. × 440. 45. Transverse section through a hair stalk, showing the number of epidermal cells adjoining it. × 440.

Growth after infection is vigorous, as is shown by the size of the hypha in Fig. 43, although the vigour of a hypha in a peach is not to be compared with that in a cherry, for instance. This figure is interesting in that two hair sockets and a stoma closely adjoining the hair sockets are shown. The two hair sockets were infected, while the stoma was not infected.

In this variety therefore, while there seems to be no obstacle in the way of stomatal infection, it is yet second in numerical and practical importance to socket infection.

Wiggins. Hairs are numerous in this variety, although not so numerous as in Kia Ora. They are evenly distributed and are separated from one another by high cushions of epidermal tissue. The cells of the latter may all be elongated, but in the larger cushions, at least, the central cells only are narrow and tall, while those at the edge are superimposed and relatively shallow. The common walls between these superimposed cells may be horizontal or inclined, those of the majority being horizontal. The sides of the cushions slope downwards somewhat steeply and cause a definite dip at the point of hair insertion. The hair stalk, which is narrow, is deeply plunged and usually does not spread at the extreme base as do the hairs of some peach varieties (Fig. 44). About six to eight cells adjoin the hair and thus provide numerous means of exit for a germ-tube passing down the socket (Fig. 45).

Stomata are rather rare and they are irregularly scattered, for while they may occur freely in one portion of a series of sections, they may need searching for in another part of the same series. Like the hairs, they occur in depressions between the epidermal cushions. The guard cells are somewhat larger than usual, but the chamber as a rule is small and may be nearly closed by projecting, thin-walled cells.

When stomatal infection occurs it is heavy, rapid, and far-reaching, the rapidity of its progress masking the effect of any hair infection that may be taking place at the same time in the vicinity. But hair infection is frequent, whereas stomatal infection, owing to the comparative rarity of stomata and their irregular grouping, is on the whole not common. Direct infection through the cuticle of a normal epidermal cell is most unusual, only one case having been found. The cuticle indeed seems resistant in character. In socket infection growth of the germ-tubes into the depression round the hair is a characteristic feature of the infection process (Figs. 46, 47, 48), and the resulting infected areas surrounding the hairs are freely to be seen in any newly diseased tissue (Fig. 49). The figure also shows the peculiar crinkling exhibited by the stalks of hairs when hyphae are passing down the socket.

Golden Eagle. The chief distinguishing feature in the skin structure of this variety is its lack of uniformity. Features characteristic of other varieties seem to occur together in one example. Thus a more or less flat

surface bearing sub-distant hairs may pass abruptly into one with denser hairs, relatively close stomata, and well-cushioned intervening epidermal spaces. But the hairs are never really crowded, and generally are thinly spaced. Stomata are scattered over the surface, and in some parts are comparatively close together, and with their large open chambers are a distinct source of weakness to the fruit. But in other parts, again, stomata may be rare. The hypoderm is thin and consists of only four to six rows of cells.

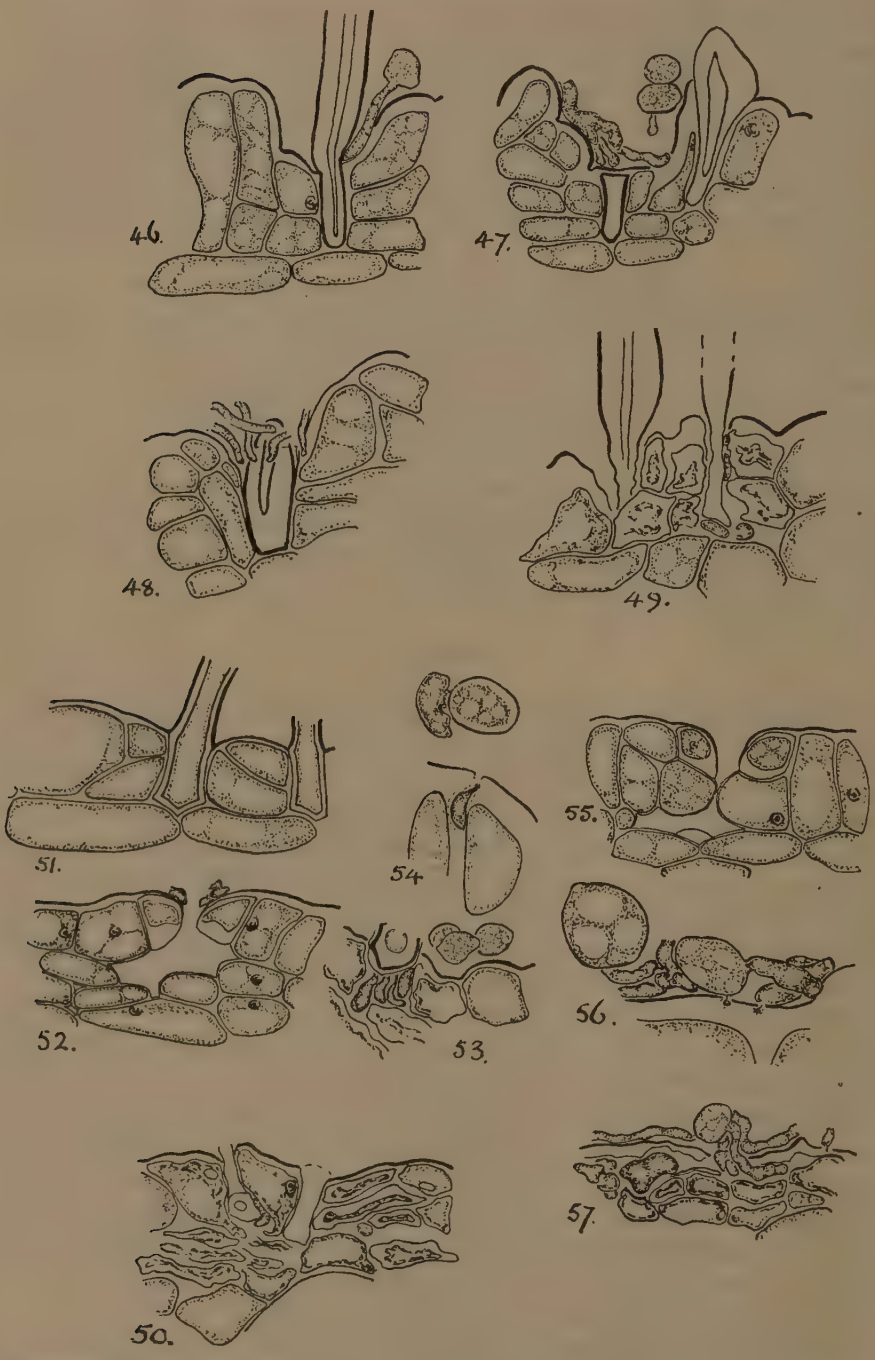
The germ-tubes of the conidia seem as much attracted to the hair sockets as in other varieties, and hair infection is much commoner than stomatal, in certain parts of the material examined as many as twenty to twenty-five hair infections taking place to one stomatal. Fig. 50 shows a typical case of collapse of the host cells as the result of direct entry down the socket, which has been cut on the slant.

In this, the last of the peach varieties to be considered, as in all the preceding ones, so large a proportion of infection takes place by a route other than the stoma that the cause of resistance or susceptibility cannot be based on stomatal characteristics alone.

Apricots.

Moorpark. The epidermis of this variety, as in most apricots, is smooth when compared with that of peaches. It is usually only a single cell deep and the cells are rather taller than wide. As the size of most of the cells is regular, a marked uniformity of surface level results. The cells near the hairs may vary in shape, but in a general view uniformity in this feature too is characteristic. The hairs are not as crowded as in the average peach, and on the whole they are more evenly spaced. Although therefore they may not retain many isolated conidia in position, they may still hold a denser mass, especially if germination has begun and the conidia are bound together. The hairs are narrower than peach hairs, but do not taper so markedly at the base where they are inserted. Their wall is thinner and the protoplasmic cavity wider. In most ways, therefore, they are slighter than the peach hair, and in addition their structure at the base bears a close resemblance to that of a normal epidermal cell (see Fig. 51). Owing to the greater distance apart of apricot hairs, conidia as a rule are not supported by them above the surface of the epidermis, but rest upon it directly. The average number of epidermal cells between the hairs is twenty-one, and about one stoma occurs to every three hairs, unless the latter are unduly far apart, when the proportion of stomata to hairs is greater.

The stomata are evenly distributed. The guard cells are supported by large thin-walled epidermal cells (Fig. 52). The cavity of the stoma ranges from small to large, but even when large it is usually shallow. One, or at



FIGS. 46–57. Figs. 46, 47, and 48. Peach, Wiggins. Stages in hair-socket infection; in the two latter figures the infection is multiple. × 440. Fig. 49. Peach, Wiggins. Young diseased area round hair bases, the latter showing the crinkling characteristic when the socket is invaded;

times two rows of rather small, but horizontally elongated, cells adjoin the epidermis. The other four or five rows of the hypoderm increase gradually in size as the general tissue of the flesh is approached, and their cells become more rounded and not dissimilar to those of the latter.

The germ-tubes do not quickly pierce the cuticle, whether at a hair base or on the smooth surface of the epidermis, but achieve it in time (Figs. 53, 54). Socket infection once established leads to as severe disease as stomatal, yet although the former is common, the number of stomata present and the slight delay in penetrating the cuticle in direct infection render stomatal infection in this variety of apricot of greater practical importance than direct infection.

Royal. This variety of apricot has fewer hairs than Moorpark, and they are thinner-walled, especially at the base within the epidermal layer. The cuticle of the epidermis is firm and well developed, and, as in the preceding variety, stomata are moderately numerous. The stomatal chamber is usually rather large and is lined with irregularly arranged parenchymatous cells which do not greatly project into the cavity. Lenticel formation is common, and this variety, like most apricots, has a faculty for irregular phellogen development over the surface. The cells of these young meristematic groups usually lie in a semicircle and include within their curve non-meristematic cells, the surface of the fruit lying plane between the two ends of the curve. The group originates as a rule about a hair or a stoma, the smaller being about hairs and the larger about stomata. The interesting feature in this development is that the hairs on stomata thus isolated have usually been recently infected, and before the hyphae have time to issue from the hair socket or stomatal chamber they are already completely cut off from the surrounding tissue by the ring of dividing cells. Division is so rapid that if the hyphae are not growing vigorously they are in danger of being suspended above the normal tissue on a low pillar of dead host cells. At times their isolation seems completely successful, but at other times, even if the suspended conidia do not succeed in passing the barrier, the germ-tubes of other conidia lying close at hand on the surface find their entry facilitated by the thinness of the walls of epidermal cells newly formed in the phellogen development. It therefore largely depends on chance whether the device is a protection or a weakness, but it often seems to be protective. By no means all the phellogen areas owe their origin to the effect of external stimulation, nor do all invading germ-tubes stimulate the

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small portions of hyphae showing at base and side of hair. × 440. Fig. 50. Peach, Golden Eagle. Infected area round invaded hair socket; section oblique. × 440. Figs. 51–4. Apricot, Moorpark. 51. Hair base and adjoining epidermal cells. × 440. 52. Stoma showing early stage of stomatal entry. × 440. 53. Hyphae emerging from base of hair-socket entry. × 440. 45. Entry directly through the cuticle of the epidermis. × 985. Figs. 55–7. Apricot, Royal. 55. Stoma small. × 440. 56. Direct entry into cuticle, early. × 985. 57. Later stage of direct entry, multiple. × 440.

development of phellogen. Yet in many cases when the two occur together they seem interdependent.

Stomatal entry as usual is common, and socket infection as already mentioned also occurs. But the latter method is not as frequent as direct cuticular entry between normal cells of the epidermis (Figs. 56, 57). Notwithstanding the prevalence of this cuticular entry, however, some slight difficulty is experienced in piercing the cuticle, for germ-tubes at times wander a little distance over the surface before succeeding in entering. At other times scarcely any germ-tube is developed, its apex being directed straight into the epidermis from the conidium (Fig. 56).

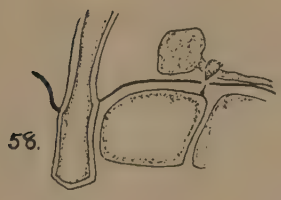
Growth of the hyphae is vigorous after infection, and their diameter, even when only at the depth of a single cell below the surface, offers a contrast to that of the germ-tubes on the surface. Yet although the width of the hyphae would signify healthy growth, they are congested and the host cells seem to withstand their passage to a considerable extent. The effect of the fungal enzyme is not felt far in advance of the hypha, for little solution of the middle lamella takes place except where the hyphal tip is in contact with host cells.

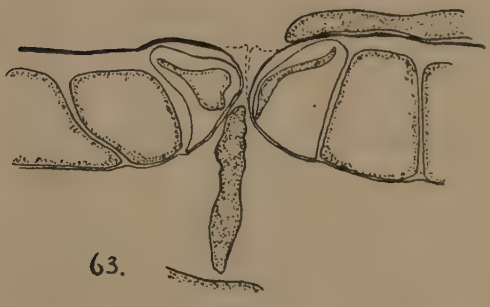
Therefore in this variety the danger of total invasion of the fruit, due to the frequency of infection through stoma and cuticle, is partly negatived by the protective character of the semi-resistant cuticle, the faculty for phellogen formation, and the resistance to solution of the middle lamella in the hypoderm.

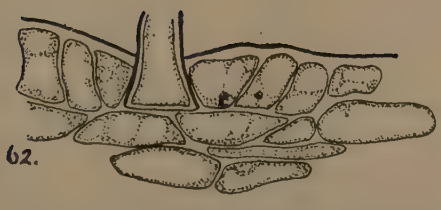
Beauge. In this variety hairs are more frequent again. On the whole the arrangement of the epidermal cells and the level of the surface resembles that of the variety Royal, but where the hairs are closely set, with only three or four cells between them, there is a tendency to cushion-formation similar to that of a peach, and with corresponding depressions where the hairs are inserted. The closer insertion of the hairs frequently results in conidia being caught singly or in groups against them, whereas in the more open parts they lie on the surface as in the usual type of apricot. Stomata occur at more or less regular intervals and are moderately numerous. They are of the normal simple type with a chamber of medium size, and when turgid the epidermal cells that bear the guard cells arch high above the fruit surface.

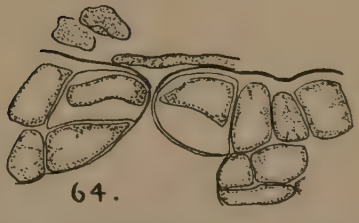
The hair is of characteristic apricot form, but spreads rather more than in most varieties in the region between the point of its insertion in the epidermis and its extreme base, and in some cases it is so enlarged in this part that the base resembles a normal epidermal cell.

Germ-tubes may travel over the surface before entry, or accomplish it as soon as the tip touches the fruit. In addition to stomatal entry, direct entry of the two kinds occurs, and if both the latter modes are considered, then direct entry in this variety is commoner than stomatal, while, of the









FIGS. 58–64. Figs. 58 and 59. Apricot, Beauge. 58. Direct entry, early. × 440. 59. Stomatal entry. × 440. Figs. 60 and 61. Apricot, Hemskirk(e). 60. Entry directly through cuticle of epidermis. × 440. 61. Stomatal entry; no directive effect of stoma on the long germ-tube. × 440. Figs. 62–4. Apricot, Roxburgh. 62. Base of hair, and epidermal cells. × 440. 63. Stomatal entry. × 985. 64. Germ-tubes passing over closed stoma. × 440.

two direct methods, that straight through the cuticle of a normal cell is more usual than that by the hair base (Figs. 58, 59).

Hemskirk(e). The cuticle of the epidermal cells is somewhat thin in this variety. Hairs and stomata occur in about average numbers and the cells supporting the guard cells, just as in the preceding variety, arch above the general level of the surface when turgid. Phellogen is developed in both large and small areas, and the frequent presence of germinating conidia on very young examples of the latter would seem to suggest that in this, as in the Royal variety, stimulation to phellogen development may at times be due to the presence of conidia or to chemical changes brought about by their germination.

All three methods of invasion take place (Figs. 60, 61), both cuticular and stomatal seeming to be equally effective. Hair infection, on the other hand, is slower. Fig. 61 shows the entry of several germ-tubes into a stoma. The conidia are part of a large group which clearly demonstrated the limitation of stomatal attraction in apricots. The germ-tubes of conidia close to or above (including at a moderate height above) the aperture were directed to it, whereas those of conidia in other positions exhibited no uniformity of direction. Even the long germ-tube shown in the figure passing above the aperture was not deflected from its course. Another conidium which rested on a cell supporting a guard cell germinated on the side away from the stoma mouth, nor did the germ-tube show any sign of subsequently changing its direction.

The appearance of all hyphae within the host tissue is suggestive of difficulty of progress. They are not under-developed, for their diameter at times is considerable, the widest noticed being those which lie between cuticle and epidermal cell. The readiness to travel in this part rather than penetrate the deeper tissues, and the frequence of branching in the hyphae, give the impression that the fungus is unable to progress freely among the cells. This does not apply so much to hyphae which have entered through stomata as to those entering through cuticle or hair socket, but the hypoderm, as a whole, including stomatal areas, gives evidence of partial resistance.

Roxburgh. This variety has a normal number of hairs, but rather more stomata than usual. The guard cells lie level with the epidermal surface and the stomatal chambers on the whole are large. The cuticle of the epidermis is thin and phellogen development general.

The variety is remarkable for the number of hair and cuticular entries. Stomatal entry is, of course, also common (Fig. 63), but when the greater number of stomata present in the variety is considered, the number of stomatal infections is not as great as might be expected. After both forms of direct infection the hyphae grow freely—distinctly more freely than in the other apricots described. The main direction followed after entry is

still horizontal, and large, shallow diseased areas lying immediately below the cuticle quickly result. But as the hyphae have comparative freedom of growth some soon turn from the main group to pass to deeper tissue.

The number of stomatal entries in the specimens examined is probably less than that of either hair or cuticular entry, and is certainly less than the number of direct entries combined. No marked directive influence is exerted on germ-tubes by the stomata unless conidia and stomata are almost in contact.

Summary.

General.

1. The morphology of the stoma is not the sole deciding factor in the determination of resistance or susceptibility in a variety, the cuticle playing an equally important, if not a more important, part.

2. In no plum, cherry, nectarine, peach, or apricot examined was the fungus unable to gain entry by piercing the cuticle, although penetration in this way might be slow and of no practical significance.

3. If stomata or lenticels were the only means of entry, then a fruit in which they are lacking should be wholly immune. The Yellow Cherry Plum is practically without either, and yet is really a susceptible variety owing to the possession of areas on the surface which have only a thin cuticle.

4. A plug of parenchymatous cells completely filling the stoma may admittedly delay infection for a time, but although several varieties of plum having most of their stomata of this form were examined, yet no case was seen in which stomatal entry was wholly prevented.

5. In a plum, if the cuticle is resistant, then the total number of stomata present is of more significance in deciding the resistance or susceptibility of the fruit than is the structure of the stoma.

6. If the cuticle of any stone fruit is really weak, neither the number nor the morphology of the stomata is of great significance, for if they also tend to weakness they can only accentuate an already established weakness; whereas if they tend to resistance, owing to the relatively small total area they cover, their effect will not materially nullify the cuticular weakness general over the whole fruit.

7. In so far as generalization is possible from the number of varieties examined, the most usual method of *effective* entry of the germ-tube is:

In plums, through the stomata;

In peaches, down a hair socket;

In cherry (only one variety examined), through the cuticle;

In nectarines, through the cuticle;

In apricots, through the cuticle or the stomata.

8. The hypoderm plays a late but often effective part in furthering resistance or susceptibility.

A synopsis of the anatomy and reactions of the different varieties studied is appended.

Plums.

Monarch. Cuticle stout but with thinner areas, stomata rare, almost completely plugged with a cone of parenchymatous cells; infection stomatal and direct, the latter more often than stomatal, owing to fewness of stomata; hypoderm stout and resistant. Result: variety more or less resistant.

Coe's Late Red. Stomata rare and irregularly grouped and therefore few stomatal entries; cuticle semi-resistant, germ-tubes entering cuticle, but with difficulty; outer half of hypoderm semi-resistant. Result: a more or less resistant variety.

October Purple. Stomata rare and irregularly grouped, completely filled with plug of parenchymatous cells, *yet can be infected*; cuticle semi-resistant but germ-tubes succeed in entering; hypoderm semi-resistant. Result: variety more or less resistant.

Burbank. Cuticular entry may be formidable owing to weak areas in the surface; stomatal infection takes place in spite of most stomata being completely plugged and the others nearly so; outer part of hypoderm semi-resistant. Result: medium resistance only, tending to susceptibility.

Japanese. Hypoderm rather weak; stomata usually fairly numerous, completely plugged, but freely entered; direct entry common but slower. Result: on the whole, more or less susceptible.

Yellow Cherry Plum. Cuticle moderately resistant only, as many thin areas are present; normal stomata practically absent and no stomatal entries found; hypoderm weak. Any resistance shown is dependent on the cuticle, but variety is really susceptible, although maturing early and thus escaping infection.

Red Cherry Plum. Stomata present and filled with a plug of cells, yet stomatal infection general; cuticle semi-resistant; hypoderm semi-resistant. Result: more resistant features than in Yellow Cherry Plum.

Cherry. Direct infection responsible for seven-eighths of total infection, and as rapid as stomatal infection; hypoderm weak. Result: variety very susceptible.

Nectarines.

Early Rivers. Stomata usually contain a plug of cells rising to the guard cells, yet stomatal infection takes place freely; direct entry more frequent than stomatal; hypoderm weak. Result: variety susceptible.

Goldmine. Some of the stomata develop later into corky lenticels which are not readily infected except at their periphery; direct entry general and almost as rapid as normal stomatal entry. Result: variety susceptible.

Peaches.

Kia Ora. Infection by the hair socket is the common method of entry; infection by the cuticle over normal epidermal cells is rarer than that by the hair socket, but no rarer than that by stomata; stomata infrequent.

Kalamazoo. Stomata moderately numerous, chambers usually open, stomatal infection ready, but second in numerical and practical significance to socket infection.

Wiggins. Stomata somewhat rare, stomatal infection may be heavy but not really general; direct infection through the cuticle of an ordinary epidermal cell rare; socket infection very common, but not as rapid as stomatal infection.

Golden Eagle. Socket infection much more common than stomatal infection.

Apricots.

Moorpark. Cuticle semi-resistant; socket infection slow but effective; stomatal infection of most significance for this variety.

Royal. Stomatal entry common; socket infection occurs, but not frequently; direct cuticular entry over ordinary epidermal cells common; cuticle semi-resistant, hypoderm semi-resistant; a faculty for phellogen formation, which is usually protective, occurs.

Beauge. Direct entry through the cuticle of a normal epidermal cell more common than socket entry; the two direct methods together more numerous than stomatal entry.

Hemskirk(e). All three methods of entry occur, cuticular and stomatal being equally effective, but socket infection slower; hypoderm semi-resistant.

Roxburgh. Socket and cuticular entry remarkably common; stomatal infection also free; hypoderm rather susceptible.

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